

SEED AND CAPSULE MORPHOLOGY IN SIX GENERA
OF HEDYOTIDEAE (RUBIACEAE): *THECAGONUM*, *NEANOTIS*, *DENTELLA*,
KOHAUTIA, *PENTODON*, AND *OLDENLANDIOPSIS*

Edward E. Terrell ¹

Research Associate
Department of Botany
National Museum of Natural History
Smithsonian Institution
Washington, DC 20013, U.S.A.

Harold Robinson

Curator
Department of Botany
National Museum of Natural History
Smithsonian Institution
Washington, DC 20013, U.S.A.

ABSTRACT

Morphological variation in the seeds and capsules of selected species of six genera of Hedyotideae (Rubiaceae) is described and illustrated by scanning electron microscopy. Oldenlandioid (trigonous) seeds occur in the genera *Dentella* and *Pentodon*. The numerous areolar tubercles in *Pentodon* seeds are shown in enlarged views. The seeds in two species of *Kohautia* have distinctive rounded areolar protrusions. *Oldenlandiopsis* has unique capsules and seeds, the latter oblate. The sulcate seeds of *Thecagonum*, an Asian segregate from *Oldenlandia*, have several rounded or elongate depressions bordered by strongly sinuous walls. *Oldenlandia strigulosa*, with similar seeds, is formally transferred to *Thecagonum*. The Asian genus, *Neanotis*, a segregate from *Anotis*, has houstonioid seeds with a hilar ridge in a ventral depression.

RESUMEN

Se describe e ilustra la variación morfológica en las semillas y las cápsulas de especies seleccionadas de seis géneros de Hedyotideae (Rubiaceae) mediante microscopía electrónica de barrido. Las semillas oldenlandioides (trigonas) ocurren en los géneros *Dentella* y *Pentodon*. Los tubérculos areolares numerosos en las semillas de *Pentodon* se muestran a gran aumento. Las semillas de dos especies de *Kohautia* tienen salientes areolares redondeados distintivos. *Oldenlandiopsis* tiene las cápsulas y semillas únicas, la última de ellas oblatas. Las semillas sulcadas de *Thecagonum*, un segregado asiático de *Oldenlandia*, tienen varias depresiones redondeadas o alargadas confinadas por paredes fuertemente sinuosas. *Oldenlandia strigulosa*, con las semillas similares, se transfiere formalmente a *Thecagonum*. El género asiático, *Neanotis*, segregado de *Anotis*, tiene las semillas houstonioides con una costilla hilar en una depresión ventral.

INTRODUCTION

This study continues investigations of seeds and capsules in the tribe Hedyotideae by means of scanning electron microscopy (SEM), studies that began with Terrell, Lewis, Robinson, and Nowicke (1986). The present paper describes and illustrates morphological variation in seeds and capsules of *Thecagonum*, *Neanotis*, *Dentella*, *Kohautia*, *Pentodon*, and *Oldenlandiopsis*. Previous studies of *Oldenlandia* seeds (Terrell & Robinson 2006) provided information about the trigonous (3-angled) seeds of that genus. Two of the genera studied here, *Dentella* and *Pentodon*, have trigonous seeds, and the other four genera have seeds with varying distinctive characteristics.

MATERIALS AND METHODS

The herbarium of the U.S. National Museum (US), Smithsonian Institution, Washington, D.C., provided most of the capsules and seeds for this study. One or more samples of each species were examined under a dissecting microscope to determine sizes, shapes and other characters. Selected samples were mounted on stubs and examined with scanning electron microscopes located at the Electron Microscope Laboratories at the Smithsonian Institution or at the U.S. Department of Agriculture, Beltsville, Maryland. The information provided for each genus includes names, synonyms, general distributions, and descriptions and illustrations of seeds and capsules.

¹Address for correspondence: 14001 Wildwood Drive, Silver Spring, Maryland 20905, U.S.A.

RESULTS AND DISCUSSION

1. DENTELLA J.R. & G. Forst., Char. Gen. Pl. 13:1775. TYPE SPECIES: *Dentella repens* (L.) J.R. & G. Forst., Char. Gen. Pl. ed. 2, 26. t. 13:1776. *Oldenlandia repens* L., Mant. Pl. 40:1767.

Distribution.—One or two species in S.E. Asia, Sri Lanka, Malesia, Taiwan, Micronesia, Polynesia (Ridsdale 1998). Adventive in coastal western Mexico (*E.J. Lott 3116* from Jalisco and other Mexican collections in herbarium US). Also locally adventive in Baltimore, Maryland (Reed 1970).

Chromosome number.—*Dentella repens*: $2n = 36$ (Raghavan & Rangaswamy 1941).

Dentella repens resembles *Oldenlandia* species, but differs in having 5-merous flowers. The plants are small creeping annual or perennial herbs. Leaves small, ca. 2–10 mm long, oblanceolate to obovate. Stipules interpetiolate, to 1 mm long. Flowers solitary, axillary, isostylous. Corolla 3–4 mm long, narrowly tubular, white. Anthers ca. 0.5 mm long. Stigmas bifid.

Capsules 2.5–4 × 2.5–3 mm, subglobose, densely hairy, crowned with calyx lobes, fully inferior, walls thin, fragile. They are reputed by Ridsdale (1998) to be indehiscent. Seeds (Table 1) numerous per capsule, 0.3–0.6 mm in diam. or slightly longer than wide, trigonous or obtusely angulate, basal face elliptical, lateral faces larger, somewhat concave, hilum punctiform, apical, areoles polygonal, walls thick, testa surface featureless (Figs. 1 A,B). The trigonous seeds are similar to those in *Oldenlandia*, thus are oldenlandioid.

Collection examined using SEM.—*Clemens 3276* (US), Indo-China. Also observed were *E.J. Lott 3116* (US) and *A. C. Sanders et al. 10597* (UCR), both from Jalisco, Mexico.

2. KOHAUTIA Cham. & Schltdl., Linnaea 4:156.1829. TYPE SPECIES: *Kohautia senegalensis* Cham. & Schltdl., Linnaea 4:156.1829.

Distribution.—The genus has about 60 species in Africa, Madagascar, and tropical Asia, with 12 species in Tropical East Africa (Verdcourt 1976). In addition, Halford (1991) described one species in Australia. Verdcourt (1989) recorded 13 species from the Flora Zambesiaca region.

Chromosome number.—Lewis (1965) reported the chromosome number of *Kohautia* as $x = 9$. He found pollen grains to be 3 to 8-colporate and relatively small, and stated that nearly all species of *Kohautia* were easily separated by their pollen from those of *Oldenlandia* and other African taxa in the tribe Hedyotideae.

Our SEM study of *Kohautia* has been restricted to one species and, therefore, the genus was excluded from Table 1. We found an unusual seed type which we consider worth reporting because of the areolar protrusions.

Kohautia coccinea Royle, Ill. Bot. Himal.: 241, t. 53/1.1835. It occurs from Africa to India. It is an annual herb with pink to purple flowers usually in spikes or racemes, corolla 5–11 mm. long, tubes narrowly cylindrical. Seeds of *K. coccinea* examined using SEM: *Burger 3545* (US), Ethiopia.

Capsules 3–5.5 mm long, oblong-ellipsoid, loculicidally dehiscent (Verdcourt 1976). Seeds 0.6–0.7 × 0.35–0.4 mm, black, obtusely angulate, hilum apical, areoles polygonal, their walls thin to rather thick, each areole containing a conspicuous large round protrusion (Fig. 1 C,D). These protrusions may occur in other species in *Kohautia*. Halford (1992) illustrated a seed of the Australian species *Oldenlandia spathulata* Halford which shows round protrusions in the areoles, but he did not comment on them. He placed *O. spathulata* in a group of three species including *O. spermacocoides* (F. Muell.) F. Muell. and *O. crouchiana* (F. Muell.) F. Muell. Specimens of these three Australian species of *Oldenlandia* were not available to us. It is suggested that *O. spathulata* may belong in *Kohautia*.

3. OLDENLANDIOPSIS (Griseb.) Terrell & W.H. Lewis, Brittonia 42:185.1990. TYPE SPECIES: *Oldenlandiopsis callitrichoides* (Griseb.) Terrell & W.H. Lewis, Brittonia 42:185.1990. *Oldenlandia callitrichoides* Griseb., Mem. Amer. Acad. Arts n.s. 8:506.1863. *Hedyotis callitrichoides* (Griseb.) W.H. Lewis, Rhodora 63:222.1961.

Distribution.—One species in West Indies, Central America and Mexico (Yucatan). Adventive in Africa (Sierra Leone), northern South America (Guyana), United States in Dade County, Florida, and Hawaiian Islands: Oahu and Maui.

A synopsis of the United States species of *Oldenlandia* (Terrell 1990) treated five species. Included

TABLE 1. Seed characters in *Thecagonum*, *Neanotis*, *Dentella*, *Oldenlandiopsis*, *Pentodon*.

	<i>Thecagonum biflorum</i>	<i>Neanotis (4 species)</i>	<i>Dentella</i>	<i>Oldenlandiopsis</i>	<i>Pentodon</i>
Number per capsule	numerous	2-20 or more	numerous	20-35	numerous
Length mm	0.3-0.6	0.5-1.3	0.3-0.6	0.3-0.5	0.3-0.5
Shape, type	ovoid, subglobose	cymbiform or shallow cup	conoidal	oblate	trigonus
Hilum	punctiform	low, linear ridge	punctiform	punctiform	punctiform
Hilum location	centric or acentric	in shallow depression	apical	centric	apical
Ventral surface, type	irregularly sulcate	reticulate	reticulate	reticulate	reticulate
Ventral surface	several small rounded or elongate depressions	polygonal areoles	polygonal areoles	polygonal areoles	polygonal areoles
Walls/borders	sinuous, conspicuous	straight/curved, not conspicuous	straight	sinuous/straight	bearing many minute tubercles

among these was *Oldenlandia callitrichoides* Grisebach, which Terrell and Lewis (1990) soon described as *Oldenlandiopsis callitrichoides* (Griseb.) Terrell & W.H. Lewis.

The plants are creeping, soft and delicate, and may be superficially confused with *Oldenlandia* species, but very few *Oldenlandia* species are creeping (versus merely prostrate).

Capsules 1.0-2.7 × 0.5-2 mm, narrowly turbinate or obconic, thin-walled, fragile, retuse or truncate, 9/10 or fully inferior, somewhat compressed, glabrous, dehiscent loculicidally and later separating into four narrow segments. These capsules differ entirely from the characteristically subglobose, indurate capsules of not only *Oldenlandia* but also from a number of other examined hedyotoid genera.

Seeds (Table 1) 20-35 per capsule, 0.3-0.5 × 0.2-0.4 mm, oblate (depressed-ellipsoid, depressed-subglobose), or obtusely angulate, hilum punctiform, centric, testa reticulate, areoles polygonal, walls sinuous or straight, surface minutely papillose (Fig. 1 E,F). The seeds are distinctive in being more or less oblate. Collection examined using SEM: E. & B. Terrell 5022 (US), Dade Co., Florida.

There are two other basic differences that also distinguish *Oldenlandiopsis* (Terrell & Lewis 1990) as a distinct genus: (1) pollen with 8-colporate apertures instead of 3(-5), (2) chromosome number $2n = 22$ ($x = 11$) instead of $x = 9$; the only other *Oldenlandia* species with $x = 11$ is *Oldenlandia microtheca* (Terrell & Robinson 2006).

4. PENTODON Hochst., Flora 27: 552.1844. TYPE SPECIES: *Pentodon pentandrus* (Schumach. & Thonn.) Vatke, Oesterr. Bot. Z. 25:231.1875. *Hedyotis pentandra* Schumach. & Thonn., Kongel. Danske Vidensk. Selsk. Naturvidensk. Math. Afh. 3:71.1827. *Oldenlandia pentandra* (Schumach. & Thonn.) DC., Prodr. 4:427.1830, non Retz.

Hedyotis halei Torr. & A. Gray, Fl. N. Amer. 2:42.1841. *Oldenlandia halei* (Torr. & A. Gray) Chapm., Fl. Southern U.S. 181.1860. *Pentodon halei* (Torr. & A. Gray) A. Gray, Syn. Fl. N. Amer. 1, 2:28.1884. The name *Pentodon halei* was created for American plants from collections prior to 1841, but plants were found to be conspecific with *P. pentandrus*.

Distribution.—Two species in Africa (see also Verdcourt 1976, 1989, Rogers 1987). Adventive in Florida and southeastern U.S. west to eastern Texas. Also adventive in Cuba, Nicaragua, and Brazil.

The chromosome number is $x = 9$ based on *Pentodon halei*, $n = 9$, $2n = 18$ (Lewis 1962); and *P. pentandrus*, $n = 9$ (Lewis 1965). Pollen is 3-aperturate and resembles most species of *Oldenlandia* (Lewis 1965).

Pentodon pentandrus var *pentandrus* is as follows: Annual or short-lived perennial fleshy herbs. Leaves lanceolate to elliptic, 3-8 × 0.3-2.5 mm. Stipules interpetiolate, fimbriate, 0.5-5 mm long. Flowers 5-merous, terminal or axillary, isostylous or heterostylous. Calyx and corolla 5-lobed, corolla funnellform. Stigmas bifid.

Capsules (Fig. 2 D) 2-4 × 2-3.5 mm, oblong, somewhat compressed, conspicuously nerved, thin-walled, fragile, loculicidally dehiscent. Seeds (Fig. 2 A-C) numerous, 0.3-0.5 mm in diam., trigonus or irregularly

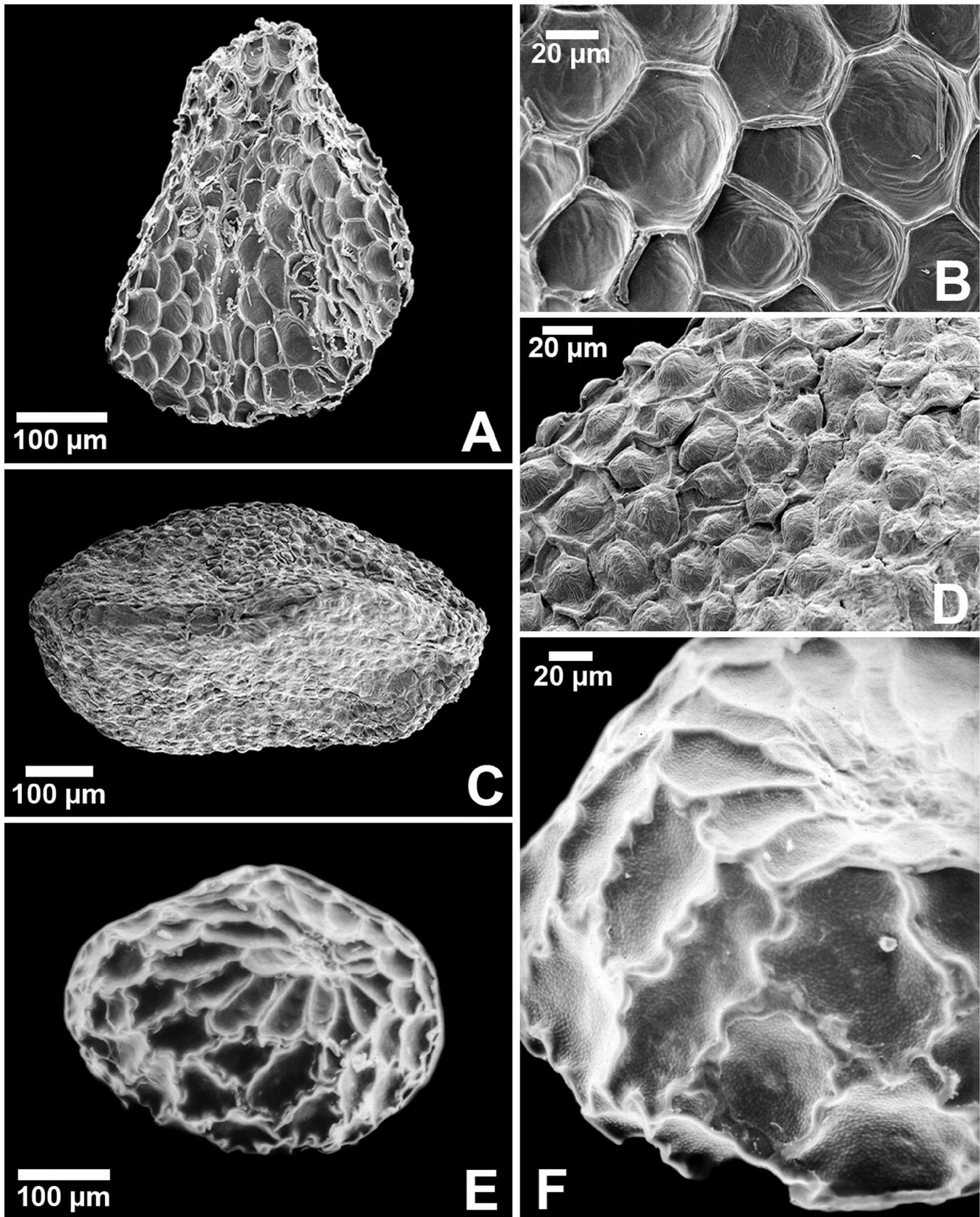


FIG. 1. Seeds examined by SEM. A–B. *Dentella repens*, Clemens 3276 (US), Indo-China. C–D. *Kohautia coccinea*, Burger 3545 (US), Ethiopia. E–F. *Oldenlandia callitrichoides*, E. & B. Terrell 5022 (US), Florida. A, end view; B, F, enlarged areoles; C, E, ventral views; D, areoles showing rounded protrusions.

and obtusely angulate, hilum punctiform, apical, testa reticulate, areoles elongate or polygonal, areole walls with numerous minute tubercles (Fig. 2 B,C). Seed collection examined using SEM: *Thieret 16435* (SMU), Louisiana.

Pentodon capsules are distinctive in being oblong with soft, compressed walls. The seeds (Table 1) are trigonous, thus appear oldenlandioid. The noteworthy feature of the seeds are the numerous minute tubercles attached to the areole walls, somewhat enlarged in Fig. 2. These tubercles were noted by Lewis, but have not been previously illustrated. Such tubercles have not been seen in any other taxon of the tribe.

5. THECAGONUM Babu, Bull. Bot. Surv. India 11:214.1969. TYPE SPECIES: *Thecagonum pteritum* (Bl.) Babu. *Gonotheca* Bl. ex DC., Prodr. 4: 429.1830 (non Raf., Med. Repos. 5:352.1808, Compositae). Babu (1969) proposed the new name, *Thecagonum*, to replace the illegitimate name, *Gonotheca* Bl. ex DC., a later homonym. Babu separated this genus from *Oldenlandia* by its having a 4-angled fruit, not terete, and seeds globose or subglobose, not angular. He recognized four species in *Thecagonum*. Specimens of the fourth species, *T. parishii* (Hook.f.) Babu, native to India and Malesia, were not available to us.

1. *Thecagonum biflorum* (L.) Babu, Bull. Bot. Surv. India 11:214.1969. *Oldenlandia biflora* L., Sp. Pl. 119.1753. *Hedyotis biflora* (L.) Lam., Tabl. Encycl. 1:272.1791.

Oldenlandia paniculata L., Sp. Pl. ed. 2. 1667.1763.

The synonymy here follows Fosberg & Sachet (1991) in their treatment of Micronesian species of *Hedyotis* in which they delimited *Hedyotis* broadly with *Oldenlandia* as a subgenus.

Distribution.—This well known species usually called *Oldenlandia biflora* has a wide distribution from India to China, Malesia, Micronesia, and Polynesia. Flora Vitiensis (Smith & Darwin 1988) stated “crevices of arid rocks along coasts,” and listed distribution as tropical Asia to Mauritius, throughout Malesia, eastward to Fiji, Tonga, Niue, and Samoa.

Collections examined using SEM.—Fosberg 39194 (US), Guam; Fosberg 33792 (USF), Marshall Islands; Anderson 2126 (US), Caroline Islands.

Chromosome number.—*Oldenlandia paniculata*: $n = 36$ (Raghavan & Ragaswamy 1941); *O. biflora*: $n = 18$ (Lewis and Oliver 1970); $2n = 54, 72$ (Selvaraj 1987).

Perennial herbs. Stems erect to prostrate. Leaves 8–40 × 3–13 mm, lanceolate, elliptic, or ovate-lanceolate. Stipules 1–2 mm, interpetiolate, margins with teeth or setae. Inflorescence terminal and axillary. Corollas broadly tubular, tubes ca. 2 mm long, lobes ca. 1 mm long.

Capsules 2–4 × 2–4 mm, subglobose, somewhat compressed, walls thin and fragile, about 4/5 to fully inferior, dehiscing loculicidally and septicidally.

Seeds (Table 1) numerous per capsule (ca. 65 in one capsule), 0.3–0.6 × 0.3–0.6 mm, ovoid, subglobose, or obtusely angulate, hilum centric, punctiform, surface with crowded, variously-sized, shallow, rounded or elongate depressions, their walls thick and strongly sinuous (Fig. 3). These depressions are entirely unlike the conventional areoles of many species, and may be described as sulcate, a term defined by Kiger and Porter (2001), as “Having one or more elongate, relatively narrow and shallow depressions (sulci).” These distinctly different seeds support the removal of *Oldenlandia biflora* from the genus *Oldenlandia* and the recognition of *Thecagonum* as a distinct genus

2. *Thecagonum strigulosum* (DC.) Terrell & H. Rob., comb. nov. BASIONYM: *Oldenlandia strigulosa* DC., Prodr. 4:427.1830.

Hedyotis strigulosa (DC.) Fosberg, Smithsonian Contr. Bot. 45:28.1980.

Hedyotis coreana H. Lév., Repert. Spec. Nov. Regni Veg. 11:64.1912.

Oldenlandia albido-punctata Merr., Philipp. J. Sci., C, 9:297.1914.

This species was not included in *Thecagonum* by Babu (1969), however, it was recognized as closely related to *Hedyotis biflora* by Fosberg and Sachet (1991). They provided a complete description of it and in their key to species distinguished *Hedyotis strigulosa* from *H. biflora* in characters of the leaves, inflorescence, and capsules. They described capsules as being firm, thick-walled, and broadly ovoid, compared to *H. biflora* which is thin-walled and subglobose. *Hedyotis strigulosa* seems not to have been transferred to *Thecagonum*, so we do so here.

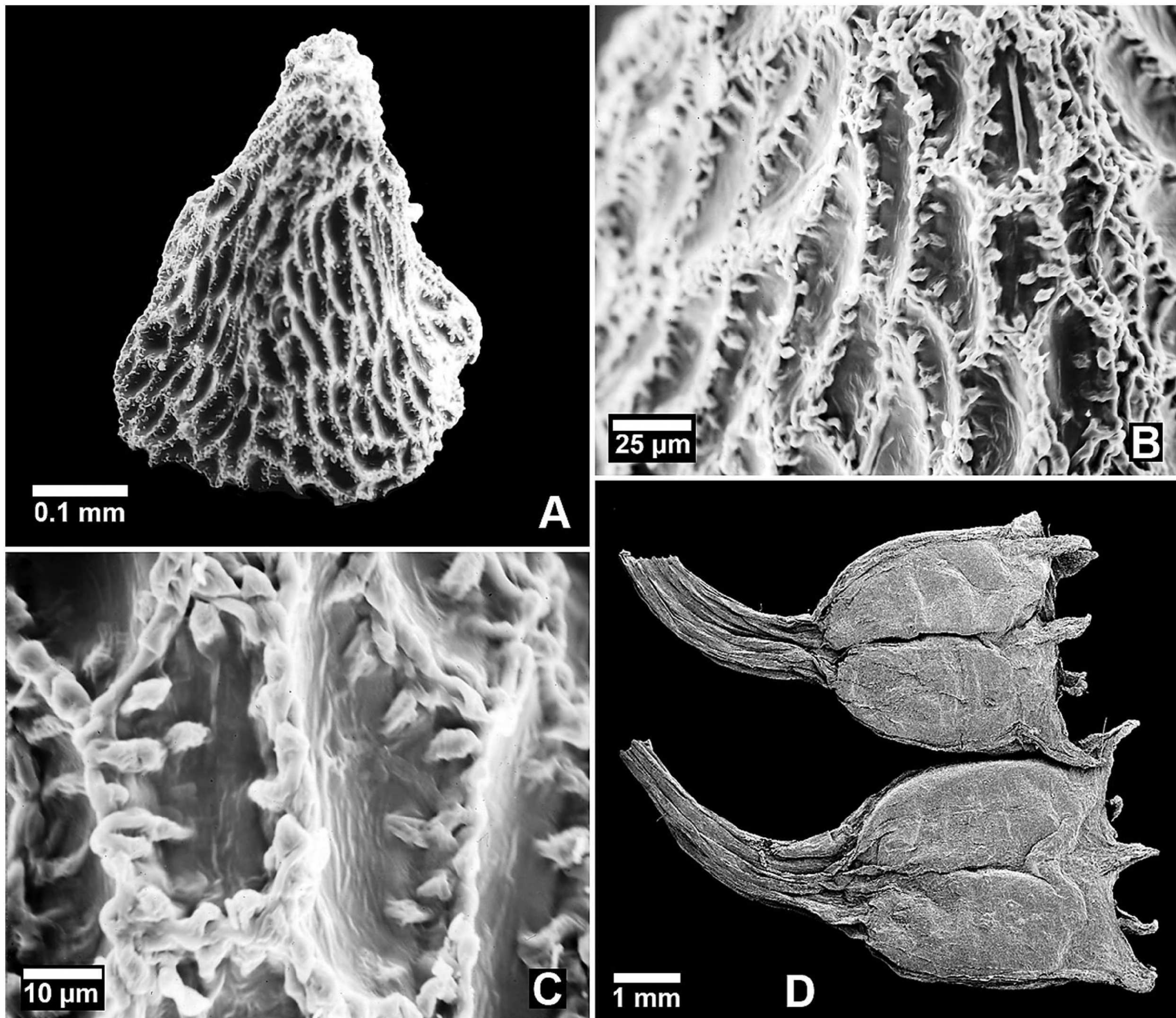


FIG. 2. Seeds and capsules of *Pentodon pentandrus* examined by SEM. A–C. *Thieret 16435* (SMU), Louisiana. D. *Lewalle 1527* (US), Burundi. A, seed, end view; B, C, enlarged areoles showing numerous tubercles; D, capsules.

Our seeds are approximately 0.4–0.6 mm long and have rounded or elongate depressions like the seeds of *T. biflora*, but differ in the seeds being mostly obtusely angulate.

Collections examined using SEM.—*Moran 4618* (US) and *Necker 362* (US), both from Guam, Marianas Islands. These two collections were cited as *Hedyotis strigulosa* by Fosberg and Sachet (1991).

3. *Thecagonum pteritum* (Bl.) Babu, Bull. Bot. Surv. India 11:214.1969. *Hedyotis pterita* Bl., Bijdr. 972.1826. *Gonothecca blumei* DC., Prodr. 4: 429.1830, nom. illeg. *Oldenlandia pterita* (Bl.) Miq., Fl. Ind. Bat. 2:193.1857.

Succulent herb to 10 cm tall. Leaves 3–6 × 0.5 cm, elliptic or lanceolate. Flowers terminal and axillary. Capsules 4–7 × 4–6 mm, oblong or obovate, somewhat compressed, walls fragile, winged, wings apparently two per capsule, to ca. 1 mm wide (Fig. 4 C). The capsules resemble those of *Pentodon pentandrus* in general shape and texture, thus they differ from the capsules of the two preceding species of *Thecagonum*. The epithet, *pterita*, refers to the winged capsules.

Seeds numerous per capsule, 0.5–0.6 × 0.4–0.5 mm, broadly ellipsoid-angulate or obtusely angulate, hilum punctiform or slightly elongate, centric, surface with variously-sized rounded or elongate depressions, walls thick, sinuous, testa densely papillose (Fig. 4 A, B). The seeds are generally similar to those of *T. biflorum*.

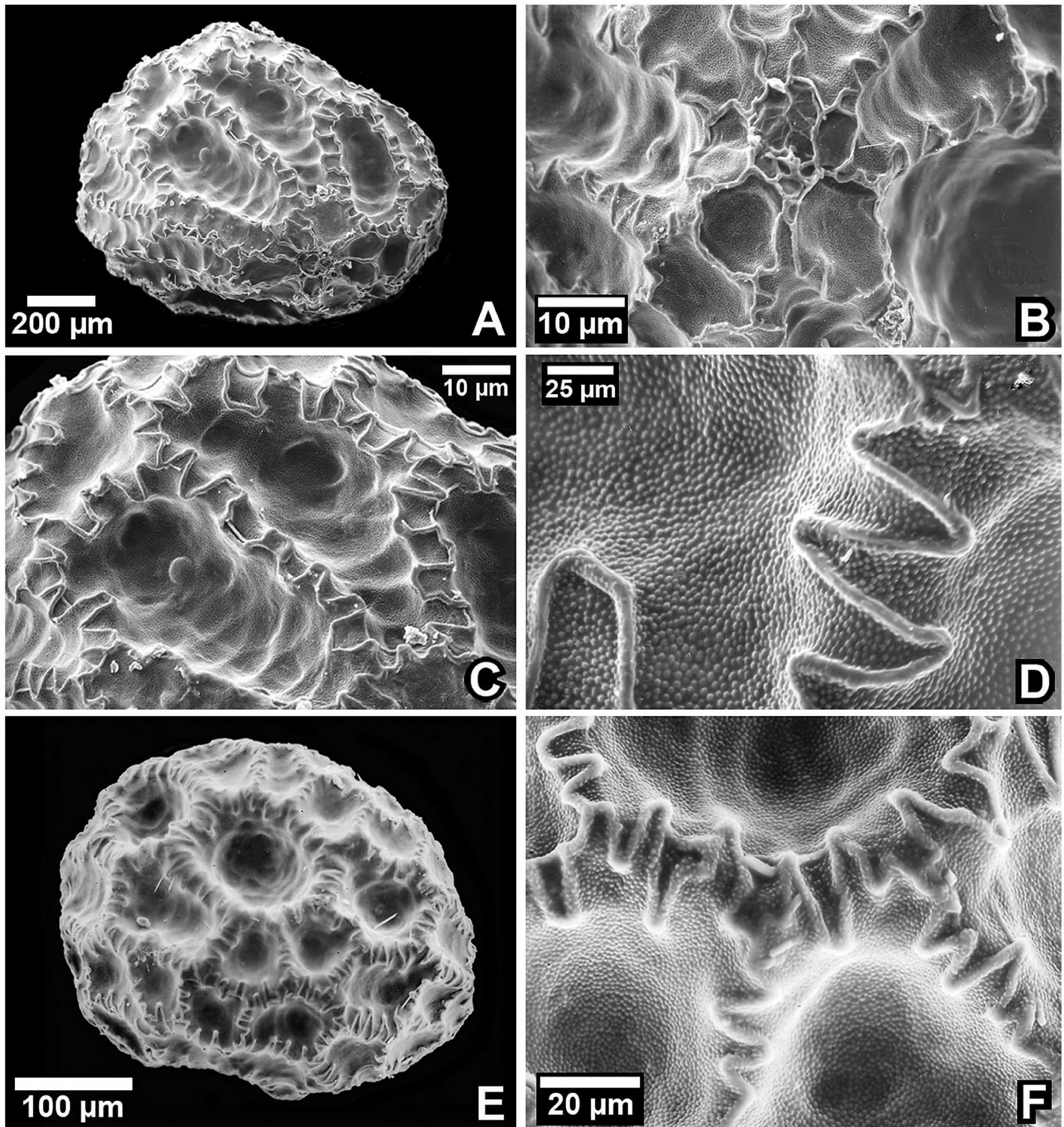


FIG. 3. Seeds of *Thecagonum biflorum* examined by SEM. A–D. Fosberg 39194 (US), Guam. E–F. Fosberg 33792 (USF), Marshall Islands. A, C, E, surface depressions and sinuous borders; B, hilar area of surface; D, F, enlargements of depressions, borders, and numerous minute papillae.

Distribution.—India to Malesia.

Collections examined using SEM.—Ramos s.n., Apr 1909 (US), Luzon, P.I.; Merrill 6730 (US), Negros, P.I.

Oldenlandia ovatifolia (Cav.) DC., Prodr. 4:427.1830. *Hedyotis ovatifolia* Cav., Icon. 6:52.1801. *Thecagonum ovatifolium* (Cav.) Babu, Bull. Bot. Surv. India 11:214.1969.

Oldenlandia nudicaulis Roth, Nov. Pl. Sp. 95. 1821. *Hedyotis nudicaulis* (Roth) Wight & Arn., Prodr. 416.1834.

This species was listed under *Thecagonum* by Babu (1969), however, its seeds lack the depressions typical of *T. biflora*, *T. strigulosa*, and *T. pterita*, and instead are reticulate with polygonal areoles like those in other

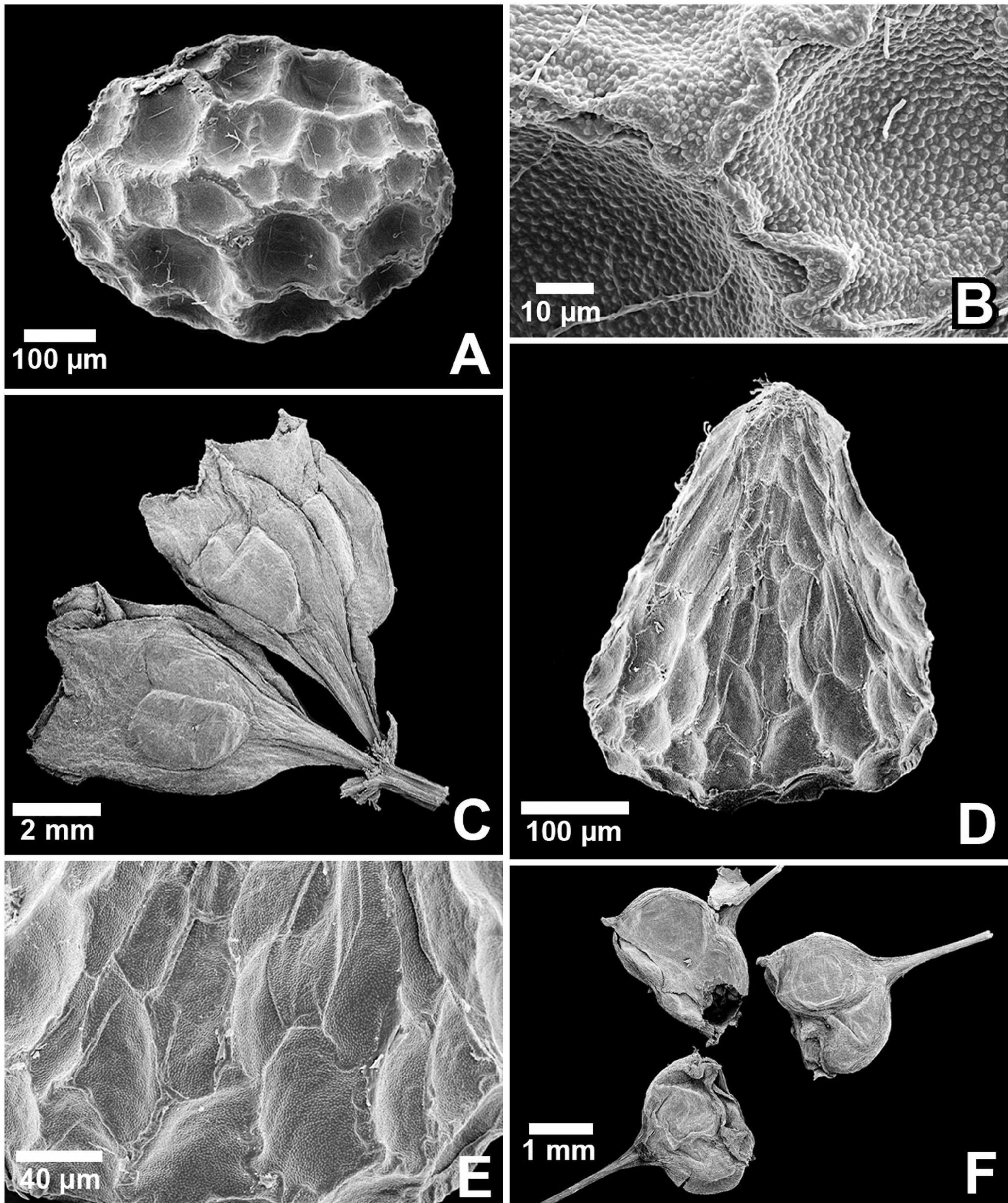


FIG. 4. Seeds and capsules examined by SEM. A–C. *Thecagonum pteritum*, A–B. Ramos s.n., Apr 1909, Luzon, P.I.; C, Merrill 6730 (US), Negros, P.I. D–F. *Oldenlandia ovatifolia*, D, E, Toroes 4448 (US), Sumatra; F, Belsher 558 (US), Upper Burma. A, depressions and sinuous borders; B, enlargements of border and minute papillae; C, F, capsules; D, seed, side view; E, enlargement of polygonal areoles.

genera. The capsules generally resemble those of some species of *Oldenlandia* (Fig. 4 F). The seeds are conoidal. We suggest that this species be retained in *Oldenlandia*.

Annual herb, stems 4–20 cm tall, leaves broadly ovate, appearing conspicuously large compared to the entire plant, inflorescence cymose, corolla tubes 0.5–1 mm long, lobes 1.5–2 mm long. Capsules 2–2.5 ×

2.5–3 mm, subglobose or slightly wider than long, walls fragile, thin, 7/8 to fully inferior. Seeds 30–40 per capsule, 0.4–0.5 × 0.4–0.5 mm, conoidal or irregularly conoidal, hilum apical, punctiform, areoles polygonal, usually longer than wide, walls thick, testa densely papillose (Fig. 4 D,E).

Distribution.—India to Java and Malesia.

Collection examined using SEM.—*Toroës* 4448 (US), Sumatra; *Belsher* 558 (US), Upper Burma. Two other collections were also studied: *Toroës* 1804 (US), Sumatra; *Toroës* 3514 (US), Sumatra.

6. NEANOTIS W.H. Lewis, Ann. Missouri Bot. Gard. 53:34.1966. TYPE SPECIES: *Neanotis indica* (DC.) W.H. Lewis, Ann. Missouri Bot. Gard. 53:38.1966. *Putoria?* *indica* DC., Prodr. 4:577.1830.

Distribution.—Southeast Asia and Malesia (Ridsdale 1998). There are 28 species in genus (Lewis 1966; Ridsdale 1998).

Lewis (1966) removed 28 species from *Anotis* and placed them in a new genus, *Neanotis*, but did not provide a description of the new genus. The validity of the name *Neanotis* has been questioned, however, we follow Saldanha and Nicolson (1976) and Ridsdale (1998) in accepting its validity. One of our reviewers (Kirkbride) advises that the name *Neanotis* is valid because there is an indirect reference to a description.

Lewis (1966) found that the pollen of *Neanotis* differs by six important characters from that of *Hedyotis* and *Oldenlandia*. He concluded that *Neanotis* pollen is distinct and differs from all other members of the Hedyotideae.

Chromosome numbers.— $x = 9$. *N. hirsuta* var. *glabricalycina* (Honda) W.H. Lewis, $2n = 36$, Taiwan (Lewis et al. 1967); *N. gracilis* (Hook. f.) W.H. Lewis, $2n = 18$, Nepal (Malla et al. 1978).

Species studied, with synonyms, and distributions are as follows:

1. Neanotis calycina (Hook.f.) W.H. Lewis, Ann. Missouri Bot. Gard. 53:37. 1966. *Anotis calycina* Hook.f., Fl. Brit. India 3:73.1880.

Distribution.—Himalayas, India, Burma (Myanmar), Vietnam, China.

Collection treated using SEM.—*Stainton* 1590 (BM), Nepal. Other examined collections not using SEM were *Stainton et al.* 7107 (BM), Nepal; *Henry* 13512 (K, US), China.

2. Neanotis hirsuta (L.f.) W.H. Lewis, Ann. Missouri Bot. Gard. 53:38.1966. *Oldenlandia hirsuta* L.f., Suppl. Pl. Syst. Veg. 127.1782.

Distribution.—Himalayas to China, Japan, Malaysia.

Collection examined using SEM.—*Mousset* 271 (US), Java.

3. Neanotis monosperma (Wight & Arn.) W.H. Lewis, Ann. Missouri Bot. Gard. 53:40.1966. *Hedyotis monosperma* Wight & Arn., Prodr. 410.1834.

Distribution.—India and Sri Lanka.

Collection examined using SEM.—*Tirvangadum* 514 (K, US), Sri Lanka. Collection examined but not using SEM: *Fosberg* 50050 (US), Sri Lanka. Approximately 30 other US collections from Sri Lanka were noted; most of these lacked mature flowers or fruit.

4. Neanotis tubulosa (G. Don) Mabb., Taxon 29:606.1980. *Oldenlandia tubulosa* G. Don, Gen Hist. 3:531.1834. *Neanotis quadrilocularis* (Thwaites) W.H. Lewis, Ann. Missouri Bot. Gard. 53:40.1966. *Hedyotis quadrilocularis* Thwaites, Enum. Pl. Zeyl. 144.1859. *Anotis quadrilocularis* (Thwaites) Hook.f., Fl. Brit. India 3:74.1880.

Distribution.—India, Sri Lanka.

Collection examined using SEM.—*Saldanha* 17811 (US), India. *Neanotis tubulosa* (formerly *N. quadrilocularis*) differs from the other three species in having a 4-loculate instead of a 2-loculate capsule and seeds with a slightly deeper depression surrounded by a thicker margin. This species has been generally accepted as congeneric with other *Neanotis* species.

Morphological data from *N. calycina* are briefly as follows: Herbaceous annual; stem 5–25 cm tall; leaves ovate-lanceolate, 0.5–3.5 × 0.2–1.5 cm, flowers in axillary or terminal cymes, corollas white, pink, or purple, infundibular-cylindrical, 2–3 mm long.

TABLE 2. Seed characters in four *Neanotis* species.

Characters	<i>calycina</i>	<i>monosperma</i>	<i>hirsuta</i>	<i>tubulosa</i>
Length mm	0.5–0.7	0.9–1.2	1.1–1.3	0.6–0.7
Thickness	thick	thick	rather thick	thick
Shape, kind	cymbiform	cymbiform	cymbiform/saucer	cymbif./shallow cup
Shape in outline	suborbicular/oblong/ell.	oblong, ell., suborbic.	suborbic./elliptic	suborbic./brdly. ell.
Compression	slight to moderate	moderate	moderate	moderate
Dorsal face	rounded/convex	strongly rounded	rounded/convex	convex
Hilar ridge	low, linear	low, linear	low, linear	low, shortly linear
Depression	medium to shallow	shallow	shallow or flattish	small cup
Margin shape	thickened/rather thin	slightly or not thickened	low/ flattish	thickened
Areoles texture	coarse	coarse	coarse	coarse
Areoles walls	indurate	indurate	indurate	indurate

The apically dehiscent capsules of *Neanotis* species are generally of a subglobose type, but differ in being either slightly longer than wide (as in *N. richardiana* (Arn.) W.H. Lewis) or wider than long (as in *N. monosperma*). They are relatively small and have comparatively few of the rather bulky seeds (ca. 2–20 per capsule).

We examined seeds of the four species by SEM (Table 2). An inclusive morphological description (Table 1) is as follows: Seeds (Fig. 5) 0.5–1.3 mm long or wide, dull black or dark brown, thick, cymbiform to shallowly cup-shaped, in outline suborbicular, oblong, or broadly elliptic, compression moderate, dorsal face strongly rounded to convex, ventral face with a low linear hilar ridge in a shallow to medium-sized depression, margin thickened or flattish, hilar ridge slightly higher to slightly lower than the bordering margin, areoles polygonal, usually appearing coarse and indurate. The seeds usually have a “chunky” appearance because the dorsal face (Fig. 5 F) is often rounded.

The seeds of *Neanotis* resemble those of *Houstonia*, particularly the *H. purpurea* group (subgenus *Chamisme*) of four species in eastern North America (Terrell 1996), but are thicker and coarser. Plants of the *Neanotis* species examined here also resemble the *H. purpurea* group in being small to medium-sized perennial (or annual) herbs with lanceolate or ovate leaves. Other data, however, do not favor a close relationship: pollen morphology is distinctly different as noted previously, and the chromosome numbers are $x = 6$ for *H. purpurea* and $x = 9$ for *Neanotis*. If the two groups originated from the same basic stock, they underwent long isolation on separate continents.

KEY TO SEEDS AND CAPSULES OF THE STUDIED GENERA

1. Seed surface not reticulate, lacking areoles, with several shallow rounded or elongate depressions _____ **Thecagonum**
1. Seed surface reticulate, areoles (cells) numerous, rounded or polygonal.
 2. Seed surface with areoles each with a large rounded protrusion _____ **Kohautia**
 2. Seed surface with areoles lacking a rounded protrusion.
 3. Seeds 3-angled (trigonal, conoidal).
 4. Seeds with areole walls bearing numerous small tubercles; capsules compressed, oblong, thin _____ **Pentodon**
 4. Seeds with areole walls lacking tubercles; capsules subglobose _____ **Dentella**
 3. Seeds compressed or ovoid, not 3-angled.
 5. Seeds oblate, lacking a hilar ridge _____ **Oldenlandiopsis**
 5. Seeds somewhat compressed, with a hilar ridge in a ventral depression _____ **Neanotis**

ACKNOWLEDGMENTS

We thank Scott Whittaker and Susann Braden, Electron Microscope Laboratory, Smithsonian Institution, for preparation of SEM illustrations, and Marjorie Knowles for preparing the figures. We also thank the curators of the herbaria cited in the text. Joseph Kirkbride and John Wiersema provided very helpful reviews of the manuscript.

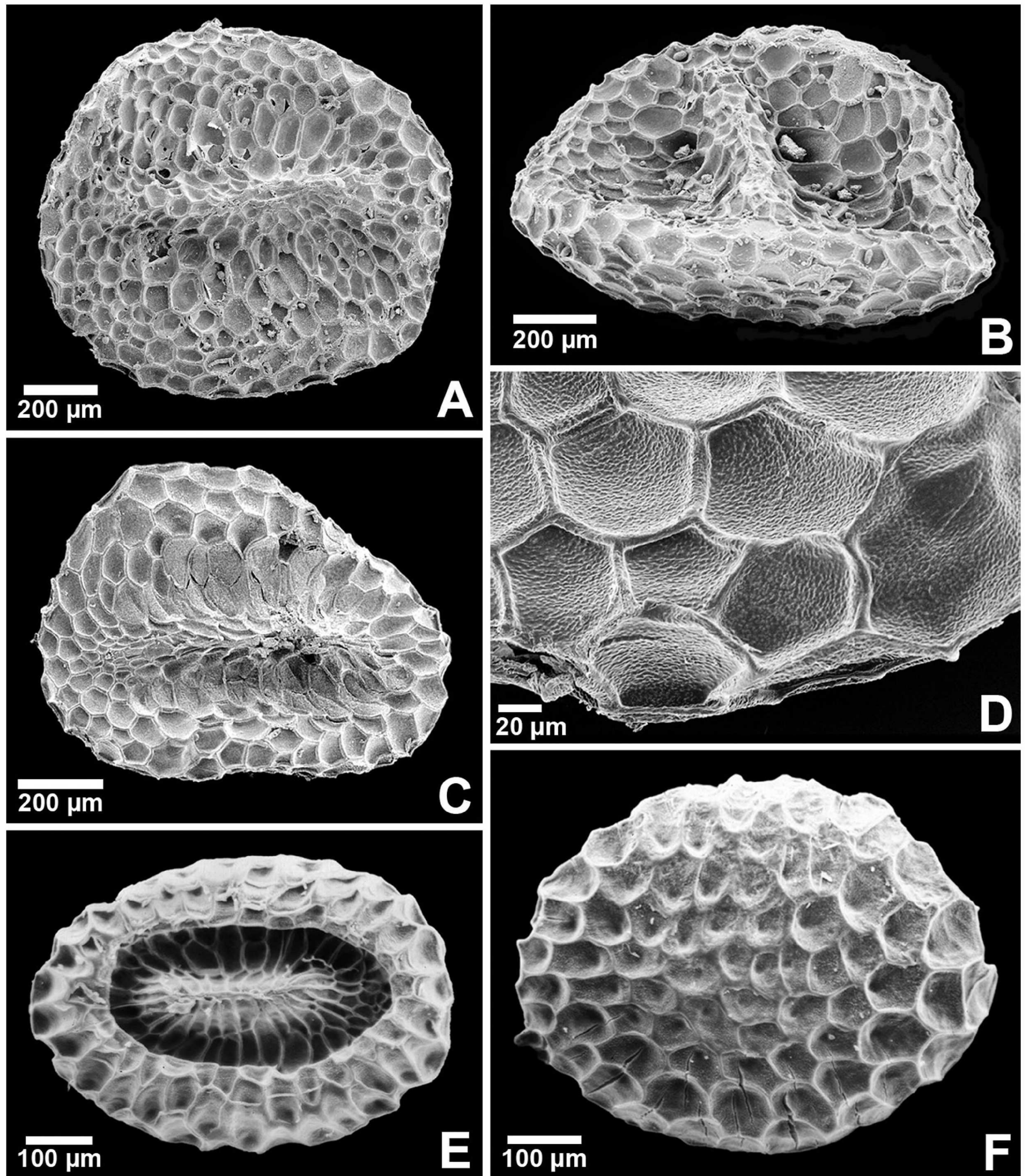


FIG. 5. Seeds of *Neanotis* species examined by SEM. A, B, *N. hirsuta*, Mousset 271 (US), Java. C, D, *N. monosperma*, Tirvangadum 514 (US), Sri Lanka. E, F, *N. tubulosa*, Saldanha 17811 (US), India. A–C, E, ventral views; D, enlargement of areoles and minute papillae; F, dorsal view.

REFERENCES

- BABU, C.R. 1969. *Thecagonum* Babu—a new generic name in Rubiaceae. Bull. Bot. India 11:213–214.
- FOSBERG, F.R. and M.-H. SACHET. 1991. Studies in Indo-Pacific Rubiaceae. Allertonia 6:191–278.
- HALFORD, D.A. 1991. The genus *Kohautia* Cham. & Schlecht. (Rubiaceae) in Australia. Austrobaileya 3: 439–442.

- HALFORD, D.A. 1992. Review of the genus *Oldenlandia* L. (Rubiaceae) and related genera in Australia. *Austrobaileya* 3:683–722.
- KIGER, R.W. and D.M. PORTER. 2001. Categorical Glossary for the Flora of North America Project. Hunt Institute for Botanical Documentation, Carnegie Mellon University, Pittsburgh, PA.
- LEWIS, W.H. 1962. Phylogenetic study of *Hedyotis* (Rubiaceae) in North America. *Amer. J. Bot.* 49:855–865.
- LEWIS, W.H. 1965. Cytopalynological studies of African Hedyotideae (Rubiaceae). *Ann. Missouri Bot. Gard.* 52:182–211.
- LEWIS, W.H. 1966. The Asian genus *Neanotis* nomen novum (*Anotis*) and allied taxa in the Americas (Rubiaceae). *Ann. Missouri Bot. Gard.* 53:32–46.
- LEWIS, W.H. and R.L. OLIVER. 1970. Chromosome numbers of Phanerogams. 3. *Ann. Missouri Bot. Gard.* 56:474.
- LEWIS, W.H., Y. SUDA, and R.L. OLIVER. 1967. Chromosome numbers of phanerogams. 2. *Ann. Missouri Bot. Gard.* 54:181.
- MALLA, S.B. et al. 1978. IOPB Chromosome number reports LIX. Presented by A. Löve. Reports by Malla et al. *Taxon* 27:55.
- RAGHAVAN, T.S. and K. RANGASWAMY. 1941. Studies in the Rubiaceae. Part 1. *J. Indian Bot. Soc.* 20:341–356.
- REED, C.F. 1970. *Dentella repens* and *Hedyotis corymbosa*, new to the United States. *Phytologia* 19:311–312.
- RIDSDALE, C.E. 1998. Rubiaceae, Tribe Hedyotideae. In: M.D. Dassanayake, ed. A revised handbook to the flora of Ceylon. Vol. XII. A.A. Balkema, Rotterdam. Pp. 236–284.
- ROGERS, G.K. 1987. The genera of Cinchonoideae (Rubiaceae) in the southeastern United States. *J. Arnold Arbor.* 68:137–183.
- SALDANHA, C.J. and D.H. NICOLSON. 1976. *Neanotis*. In: Flora of the Hassan District, Karnataka, India. Amerind Publ. Co. Pvt. Ltd., New Delhi. P. 583.
- SELVARAJ, R. 1987. Karyomorphological studies in South India Rubiaceae. *Cytologia* 52:343–356.
- SMITH, A.C. and S.P. DARWIN. 1988. Rubiaceae, vol. 4, *Hedyotis*. In: A.C. Smith, *Flora Vitiensis Nova*. Pacific Tropical Botanical Garden, Kauai, Hawaii. Pp. 352–359.
- TERRELL, E.E. 1990. Synopsis of *Oldenlandia* (Rubiaceae) in the United States. *Phytologia* 68:125–133.
- TERRELL, E.E. 1996. Revision of *Houstonia* (Rubiaceae-Hedyotideae). *Syst. Bot. Monogr.* 48:1–118.
- TERRELL, E.E. and W.H. LEWIS. 1990. *Oldenlandiopsis* (Rubiaceae), a new genus from the Caribbean Basin, based on *Oldenlandia callitrichoides* Grisebach. *Brittonia* 42: 185–190.
- TERRELL, E.E. and H. ROBINSON. 2006. Taxonomy of North American species of *Oldenlandia* (Rubiaceae). *Sida* 22:305–329.
- TERRELL, E.E., W.H. LEWIS, H. ROBINSON, and J.W. NOWICKE. 1986. Phylogenetic implications of diverse seed types, chromosome numbers, and pollen morphology in *Houstonia* (Rubiaceae). *Amer. J. Bot.* 73:103–115.
- VERDCOURT, B. 1976. Rubiaceae (Part 1), *Kohautia*, *Oldenlandia*. In: R.M. Polhill, ed. *Flora of Tropical East Africa*. Crown Agents, London. Pp. 228–242; 268–315.
- VERDCOURT, B. 1989. Rubiaceae, Vol. 5, part 1. In: E. Launert, ed., *Flora Zambesiaca*. Flora Zambesiaca Managing Committee.